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Seasonal Effects on Female Fecundity and Male Sperm Availability in a Thermally Stable Temperate Population of Sailfin Mollies (*Poecilia latipinna*)

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ABSTRACT.—Fish species from temperate climates exhibit seasonal variation in reproduction triggered by abiotic variables such as day length and temperature. The sailfin molly *Poecilia latipinna* occupies habitats in the southern temperate zone in North America, but little is known about seasonal patterns in reproductive parameters such as female egg production and male sperm production, especially in spring-fed habitats. Males and females were collected monthly for 21 mo to: (1) examine the seasonal patterns in egg availability, (2) examine the relationship between female size and fecundity, (3) examine seasonal patterns in male sperm availability and (4) examine the relationship between male size and sperm availability. We found that reproductive investment varied seasonally in both males and females in a population of sailfin mollies occupying a spring-fed habitat. Because both egg and sperm production can be energetically costly, individuals may reduce costs associated with reproduction by reducing the availability of ready gametes during the time of year when mating is infrequent.

INTRODUCTION

Many fish species that occupy temporally variable environments exhibit seasonality in reproduction (Winemiller, 1989). Species from higher latitudes generally produce young during a relatively brief period of time (Winemiller and Rose, 1992), whereas species from lower latitudes (tropics and temperate areas) may produce young over a longer period of time (Constantz, 1979; Hubbs, 1982; Winemiller, 1989; Winemiller and Rose, 1992). In variable environments, coordinating reproduction to environmental cues can optimize allocation of available energy to reproduction (Migaud *et al.*, 2010).

Fishes in the family Poeciliidae are livebearers and occupy a variety of tropical and temperate habitats. Most research examining seasonal variation in reproduction at temperate latitudes has focused on seasonal variation in fecundity of females (*e.g.*, Machado *et al.*, 2002; reviewed in Constantz, 1989; but *see* Grier, 1981; Burns, 1985). For example, reproduction in livebearing fish from temperate climates often coincides with day length and temperature (*e.g.*, Winemiller and Rose, 1992), which typically correspond to high food availability (*e.g.*, Love *et al.*, 1991; Sarma *et al.*, 2005). Longer photoperiod can lead to increased percentages of females with developing embryos, increased production of yolked eggs and larger broods (Hubbs, 1964; Burns and Flores, 1981; Burns, 1985; Winemiller, 1993). Higher temperatures are associated with a decrease in the interbrood intervals of female sailfin mollies *Poecilia latipinna* (Snelson *et al.*, 1986), and females produce fewer offspring during the winter months, although the exact months may vary by population (Farr and Travis, 1986; Snelson *et al.*, 1986).

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Some livebearing fish species occupy spring-fed habitats that can provide greater environmental stability compared to other habitats within the same geographical area. The degree to which livebearing species occupying spring-fed habitats vary in reproduction across seasons has only been addressed in a few studies. For example, *Gambusia marshi* exhibits longer reproductive periods in spring-fed habitats characterized by relatively constant temperatures across seasons (Meffe, 1985). However, the reproductive period is not longer in *Xiphophorus pygmaeus* from spring-fed habitats with temperature fluctuations (Morris and Ryan, 1992). While female *Poecilia latipinna* from temperate North America are typically gravid from Mar.–Oct. (Hubbs, 1964; Travis, 1994), the potential influence of relatively constant spring-fed habitats on this reproductive period has not been evaluated.

There is relatively little known about how male reproductive allocation varies seasonally in temperate livebearing species compared to females, although there have been a few studies of male livebearing fish from tropical and temperate latitudes. For example, males of the livebearing fishes *Alfaro cultratus*, *Phallichthys amates* and *Poecilia gillii* from tropical rainforest streams in Costa Rica and *Poecilia mexicana* from temperate headwater streams in northeast Mexico appear to be reproductively active year-round based on the testes' conditions (Monaco *et al.*, 1981; Winemiller, 1993). However, mating and reproduction are not necessarily correlated since female livebearers are able to store sperm (Farr, 1989). Regardless, male reproductive allocation has not been evaluated for temperate livebearing fish; and the potential for environmentally stable spring seep habitats to further influence reproductive allocations in these fish has also not been addressed.

We investigated seasonal patterns of female fecundity and male sperm reserves in an introduced population of *Poecilia latipinna*. The fish used in this study were collected from Spring Lake, TX, a constant-temperature spring in southern temperate North America. *Poecilia latipinna* was introduced to Spring Lake during the 1930s and originated from populations in Florida and Louisiana (Brown, 1953). The Spring Lake population is located in the headwaters of the San Marcos River (29.893°N, 97.931°W) where there is constant flow of clear water characterized by stable nutrient availability and chemical properties and a constant temperature of 21–23 C (Groeger *et al.*, 1997). We predicted that female *P. latipinna* in the Spring Lake population would exhibit longer reproductive periods if water temperature is an important variable regulating reproduction in this species. We also predicted that variation in sperm production by male *P. latipinna* would mirror the patterns observed in female gravidity.

METHODS

Female *Poecilia latipinna* were collected using dipnets once each month from Sept. 2005–May 2006 (n = 193) and twice each month from Jun. 2006–Jun. 2007 (n = 795). Females were euthanized by adding clove oil to water until females were unconscious. After euthanization, females were preserved in 10% formalin. Each female was measured for standard length (SL, mm) and dissected to remove and count the embryos and eggs present within several days of capture (2005–2006 collections). In addition to the methods used in 2005–2006, embryos from females collected in 2006–2007 were also enumerated by developmental level according to the Poeciliid Development Classification System (early developing embryo = stages 5–7 from Haynes (1995); late developing embryo = stages 8–11, Haynes, 1995). Unfertilized eggs were included in counts but were not scored for yolking.

Male *Poecilia latipinna* were collected using the same methods used for females, although they were collected only at the beginning of each month from Jul. 2005–Jun. 2006 (n =

TABLE 1.—Seasonal variation in the frequency of gravid individuals, standard length (SL, mm) and fecundity (*i.e.*, number of eggs present) for female *Poecilia latipinna* collected from Spring Lake, TX, Sept. 2005–Jun. 2007

Season	n	% gravid	Fecundity (mean \pm SE)	Gravid female SL (mean \pm SE)	Non-gravid female SL (mean \pm SE)
Nonmating	354	4.8	20.5 \pm 2.0	37.7 \pm 1.1	28.8 \pm 0.3
Early mating	153	69.3	18.9 \pm 1.2	36.1 \pm 0.7	28.8 \pm 0.7
Mid mating	283	66.4	17.1 \pm 1.0	34.8 \pm 0.6	28.9 \pm 0.5
Late mating	198	14.7	14.2 \pm 1.9	34.2 \pm 1.3	31.3 \pm 0.5

298). Upon collection, males were measured for SL (mm) and sperm was removed using established protocols (Aspbury and Gabor, 2004a, b). Males were placed along the edge of a shallow Petri dish lined with wet cotton with their ventral side up. Gentle pressure was applied to the side of the male, going from behind the eye laterally to the base of the anal fin. Spermatozeugmata (mature sperm bundles) came out at the base of the gonopodium and were collected by using an aspirator. The aspirator consisted of an aspirating mouthpiece attached to airline tubing that was then connected to a small (5-cm) glass tube with a 1–200 μ l gel-loading pipette tip attached at the end. This process was repeated on each male until no more spermatozeugmata were expelled from the male. The spermatozeugmata were placed into a microcentrifuge tube with 100 μ l of 0.9% saline solution (0.9 g of NaCl per 100 ml of water), and repeatedly drawn up and expelled from a pipette to distribute sperm cells evenly. Sperm cells were counted five times on an improved Neubauer chamber hemocytometer (Reichert, Buffalo, NY) under 400 \times magnification. The total number of sperm cells was calculated by multiplying the mean cell count by the sample's initial volume (100 μ l) and dividing by the volume of the hemocytometer (0.1 μ l). Sperm counts were made blind to the identity of the males. After sperm extraction, males were maintained at Texas State University in 38-l (54 \times 29 \times 33 cm) and 53-l aquaria (76 \times 32 \times 32 cm).

STATISTICAL ANALYSES

Monthly data were grouped by reproductive season based on the timing of gravid *Poecilia latipinna* female collection (Table 1) and on previous studies (Hubbs, 1964; Travis, 1994): nonmating (Nov.–Feb.), early mating (Mar.–Apr.), mid mating (May–Aug.) and late mating (Sept.–Oct.) seasons. To control for possible year effects, we included year as a random factor in analyses that had data from both years of female collections in all general linear models (GLM, year 1 = Sept. 2005–May 2006, year 2 = Jun. 2006–Jun. 2007). Because females continue to grow after sexual maturity and female SL is linked to variation in fecundity (reviewed in Travis, 1994), we first examined changes in female SL across seasons using analysis of variance (ANOVA) with female SL (log transformed) as the dependent variable, season as a fixed factor and year as a random factor. We then used post hoc paired comparisons (Tukey highly significant difference, HSD) to compare mean female SL among the seasons. The frequency of gravid females was compared among seasons using a binary logistic regression with the total number of embryos and eggs (*i.e.*, presence/absence) as the dependent variable, season and year as independent variables and female SL (log transformed) as the covariate. We analysed data from gravid females to determine whether fecundity varied across seasons, years and with female SL using a GLM (normal distribution, identity link function) with total number of embryos and eggs (log transformed) as the dependent variable, female SL (log transformed) as a covariate, year as a random factor,

season as a fixed factor and the season by female SL interaction. For data from year 2, we also examined whether the stage of embryo development was associated with female SL or season using a multinomial logistic regression with stage (early developing embryo = stages 5–7 from Haynes (1995); late developing embryo = stages 8–11) as the dependent factor, season as the independent factor, female SL (log transformed) as a covariate and a season \times female SL interaction.

We conducted analyses to determine whether there was significant variation in the frequency of *Poecilia latipinna* males with sperm across seasons using a binomial logistic regression on male sperm (*i.e.*, presence/absence) as the dependent variable, season as the independent variable and male SL as the covariate. We analyzed males that had sperm using GLM (normal distribution, identity link function) with sperm counts as the dependent variable, male SL as a covariate, season as the independent variable and the season by male SL interaction. We did not examine male SL across seasons because male *P. latipinna*, unlike females, grow little after sexual maturity (reviewed in Travis, 1994). Alpha was set at 0.05 and all tests were two-tailed.

RESULTS

There was significant variation in female SL across seasons (ANOVA, $F_{(3,822.5)} = 9.11$, $P < 0.001$). Females collected in the nonmating months were significantly smaller than females collected during all of the mating season months except for the late mating season of year 1 (Tukey HSD, $P < 0.05$, Fig. 1). Female SL did not differ for females collected in the mating season (Tukey HSD, $P > 0.05$). Year did not contribute significantly to variance in female SL. The full model for the frequency of gravid females found significantly more variation than the reduced model ($-2 \log \text{likelihood} = 254.92$, $df = 8$, $P < 0.001$). The frequency of gravid females varied across seasons (Wald $X^2 = 175.62$, $df = 3$, $P < 0.001$), years (Wald $X^2 = 52.31$, $df = 1$, $P < 0.001$) and female SL (Wald $X^2 = 48.49$, $df = 1$, $P < 0.001$, Table 1). More females from year 1 were gravid than females from year 2. The frequency of gravid females was higher in the mid- and late mating seasons compared to the early and nonmating seasons, and, in general, larger females were more likely to be gravid. However, there was also a significant interaction between female SL and season on the frequency of gravid females present in the sample (Wald $X^2 = 9.58$, $df = 3$, $P < 0.023$), as larger gravid females in the late mating season were not more frequently encountered than smaller gravid females (Table 1).

The number of embryos and eggs in gravid females did not vary by season ($F_{3,49.7} = 2.52$, $P = 0.069$). Larger gravid female *Poecilia latipinna* had significantly greater numbers of embryos and eggs compared to smaller females regardless of season ($B = 2.68$, adjusted $r^2 = 0.649$, $F_{1,320} = 119.11$, $P < 0.001$). In addition, there was a significant interaction between female SL and season on the total number of embryos and eggs in gravid females among seasons ($F_{3,320.4} = 4.46$, $P = 0.004$). Year did not contribute to variation in the number of embryos and eggs. The full model for the development of embryos in gravid females found significantly more variation than the reduced model ($-2 \log \text{likelihood} = 42.20$, $df = 14$, $P < 0.001$). Furthermore, there was significant variation in the development of the embryos in gravid females across seasons (Wald $X^2 = 46.82$, $df = 6$, $P < 0.001$; Table 2). The frequency of early developing embryos peaked in the early and mid-mating seasons, whereas the frequency of gravid females with unfertilized eggs was higher during the nonmating season. Embryo development did not vary with female SL (Wald $X^2 = 7.23 \times 10^{-7}$, $df = 2$, $P = 1.00$), and there was no interaction between female SL and season (Wald $X^2 = 3.69$, $df = 6$, $P = 0.719$).

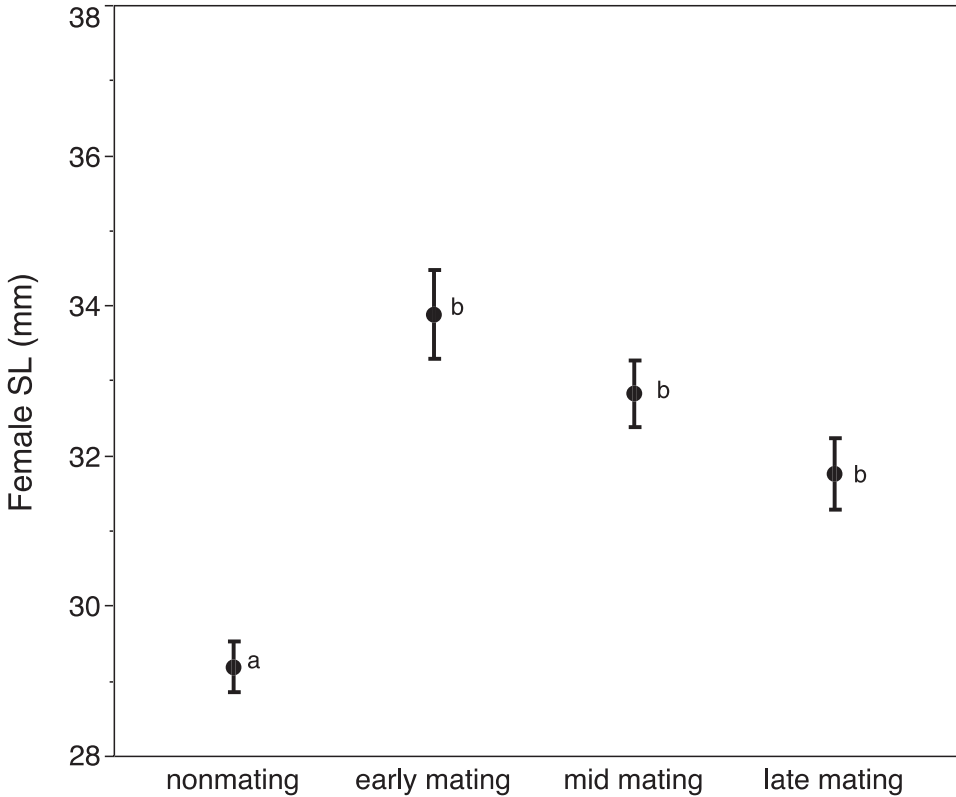


FIG. 1.—Mean (± 1 SE) standard length (mm) of female *Poecilia latipinna* collected from Spring Lake, TX, from Sept. 2005–Jun. 2007. Individuals were classified by reproductive season depending on month of capture according to the following: nonmating (Nov.–Feb.), early mating (Mar.–Apr.), mid mating (May–Aug.) and late mating (Sept.–Oct.). Means with the same letter designations were not statistically different at $\alpha = 0.05$

The frequency of male *Poecilia latipinna* with sperm varied by season (Wald $X^2 = 39.55$, $df = 3$, $P < 0.001$; Table 3). Male *P. latipinna* were more likely to have sperm in the early and mid-mating seasons compared to the late and nonmating seasons, but the frequency of males with sperm did not differ based on male SL (Wald $X^2 = 0.58$, $df = 1$, $P = 0.448$); and there was no significant interaction between male SL and season (Wald $X^2 = 7.76$, $df = 3$, $P = 0.051$). The number of sperm also varied in males with sperm ($F_{3,134} = 15.00$, $P = 0.002$).

TABLE 2.—Seasonal variation in the frequency of embryos at different stages of development collected from female *Poecilia latipinna* in Spring Lake, San Marcos, TX Sept. 2006–Jun. 2007

Season	% unfertilized	% early developed	% late developed
Nonmating	100	0	0
Early mating	77	20	3
Mid mating	26	55	19
Late mating	0	42	58

TABLE 3.—Seasonal variation in sperm availability (sperm number, sperm cells $\times 10^5$) and standard length (SL, mm) of male *Poecilia latipinna* collected from Spring Lake, San Marcos, TX Jul. 2005–Jun. 2006

Season	n	% sperm	Sperm # (mean \pm SE)	Male SL with sperm (mean \pm SE)	Male SL no sperm (mean \pm SE)
Nonmating	106	34.0	33.30 \pm 11.03	27.53 \pm 0.95	29.24 \pm 0.79
Early mating	60	85.0	61.65 \pm 10.32	28.28 \pm 0.78	30.61 \pm 2.95
Mid mating	94	48.9	84.37 \pm 14.62	26.98 \pm 0.93	24.88 \pm 0.69
Late mating	38	23.7	2.40 \pm 0.99	30.04 \pm 2.28	26.75 \pm 0.98

Males with sperm had more sperm in the early and mid mating seasons compared to the late and nonmating seasons (Table 3, Fig. 2). Finally, larger males had greater sperm counts than smaller males ($B = 320903$), and this effect did not vary by season ($F_{1,134} = 4.74$, $P = 0.030$).

DISCUSSION

This study sought to clarify variation in reproduction in a population of *Poecilia latipinna* from a constant temperature spring in a temperate climate. In spite of the constant conditions of this environment, we found seasonal variation in both male and female reproductive investment. Female fecundity was high throughout most of the early and mid mating seasons. The peak in sperm number also occurred in the early and mid mating seasons. Sperm numbers in the late mating season were similar to the nonmating season. Given the constant year round water temperatures in Spring Lake, increasing day length may explain the initial increase in sperm number; but it does not explain further changes in sperm number. However, this pattern does not necessarily contradict that day length is important. Photoperiod is considered the most reliable environmental cue used for reproduction in temperate climates (reviewed in Migaud *et al.*, 2010). In addition, different species use different day length cues to maintain their reproductive cycles (reviewed in Migaud *et al.*, 2010). Thus, sperm production and female fecundity in *P. latipinna* would not necessarily show linear changes with day length despite the importance of day length as a factor that influences reproductive condition. The reproductive season observed in this study is similar to populations of *P. latipinna* from Florida (Travis, 1994). Given the environmental differences between Florida and Texas, day length may be the most consistent variable between the two environments to explain the similar reproductive seasons.

Interestingly, the peak in sperm availability coincided with the average peak rainfall in San Marcos, TX, in May (NOAA, 2000). Other studies of livebearing fish have suggested that reproduction may coincide with peaks and dips in precipitation (*e.g.*, Reznick, 1989; Morris and Ryan, 1992; Winemiller, 1993). The possibility that *Poecilia latipinna* synchronizes its reproduction with the wet season in this population seems less likely because the San Marcos River flows year round with relatively small difference in flow rates between the wettest and driest months (the wettest month (Jul.) flow rate is 17% higher than the flow rate for the driest month (Jan.); unpublished data). However, reproduction may synchronize with other environmental variables that coincide with rainfall. Rainfall and day length both have been found to coincide with food availability (*e.g.*, Reznick, 1989; Winemiller, 1993), a necessity for increasing reproductive investment. Algae, the primary food source of *P. latipinna* (Taylor *et al.*, 2001) require light and nutrient availability. In addition to variation in light, it

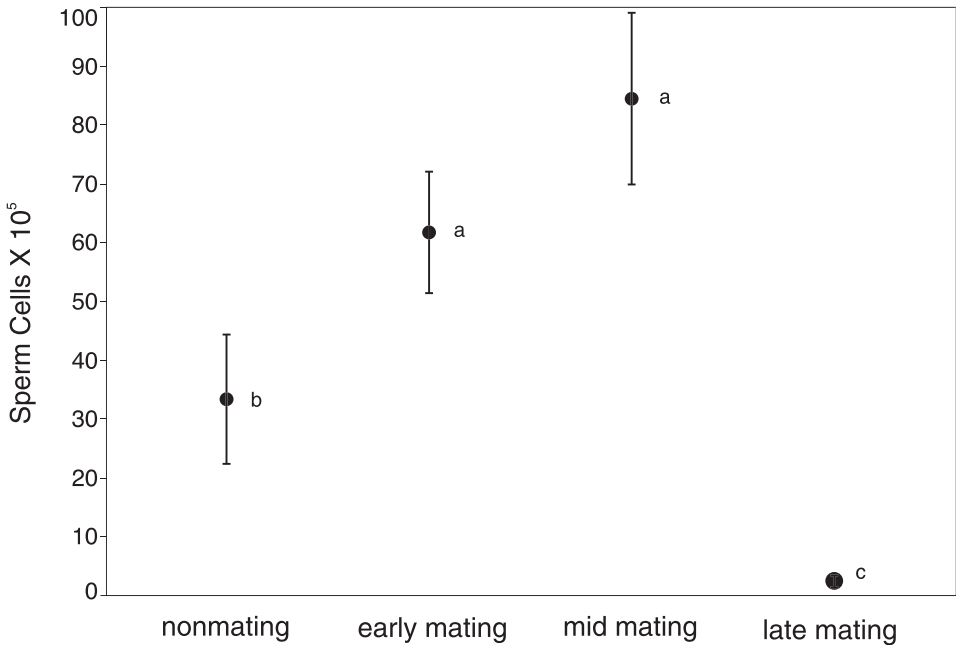


FIG. 2.—Mean (± 1 SE) sperm cells from male *Poecilia latipinna* collected from Spring Lake, TX, from Sept. 2005–Jun. 2007. Individuals were classified by reproductive season depending on month of capture according to the following: nonmating (Nov.–Feb.), early mating (Mar.–Apr.), mid mating (May–Aug.) and late mating (Sept.–Oct.). Means with the same letter designations were not statistically different at $\alpha = 0.05$.

is possible that nutrient availability in Spring Lake varies seasonally from decomposition of organic matter or surface runoff after rainfall.

The thermally stable environment that served as the focus in our study is one of many environments where *Poecilia latipinna* occurs. *Poecilia latipinna* has a native distribution from the brackish waters of southern Mexico near Rio Tuxpan and along the Gulf of Mexico through North Carolina (Hubbs *et al.*, 1991). Such a wide distribution demonstrates the species' tolerance of varying temperatures and water chemistries. Even though the population in Spring Lake occurs in a stable environment, *P. latipinna* may continue to synchronize reproduction seasonally based on cues used within its native distribution. However, other studies of *P. latipinna* have found local adaptation in other characteristics, including body size (reviewed in Travis, 1994) and mating behavior (*e.g.*, Gabor and Ryan, 2001; Gumm and Gabor, 2005). The population in Spring Lake was introduced during the 1930s (Brown, 1953). Without strong selection against seasonal reproduction, this may not be enough time for local adaptation in Spring Lake. Future studies investigating seasonal reproduction in native populations of *P. latipinna* in stable environments will help determine whether seasonal variation in Spring Lake is a characteristic of this population's introduction, or whether seasonal variation in thermally stable environments is a general characteristic of this species.

Although fecundity of female *Poecilia latipinna* was not affected by season, the frequency of gravid females varied by season, with the greatest number of gravid females occurring in

the early mating season. In prior studies of livebearing fish in temperate climates, temperature and day length have been the primary factors suggested for variation in reproduction (Constantz, 1989). Populations of *P. latipinna* from brackish marshes in Florida showed two peaks in reproduction measured by the proportion of immature males present, one in May–Jun. and another in Aug.–Sept. (Snelson, 1984). In Spring Lake, where the water temperature is constant throughout the year, similar peaks in reproduction may occur within the mating season. However, this study measured the proportion of gravid females present instead of juvenile abundance; thus, peaks in reproductive output may not be as evident from our data.

Male *Poecilia latipinna* had the most sperm available during the early mating season, although there was no difference in sperm counts between the late and nonmating season. In contrast, previous work with *P. mexicana* has shown that males of this species have lower sperm reserves during the mid mating season (Monaco *et al.*, 1981). The proportions of male *P. latipinna* with sperm and gravid female *P. latipinna* were both low in the nonmating season. During the mid mating season, more females had eggs than males had sperm and some gravid females also had maturing embryos. Although sperm and egg availability differed in frequency during the early and late mating seasons, male sperm number demonstrated seasonal variation similar to the variation in female fecundity and peaked during the early mating season. By synchronising sperm availability to the time of year when females are most fecund, males may reduce costs associated with spermatogenesis. As the mating season progresses and the likelihood of fertilizing a female's eggs decreases, males may become less discriminating and increase sperm expenditure during female encounters. Whereas the number of males with sperm and number of gravid females was lower during the late mating season, the reduction in male sperm availability may reflect increased sperm expenditure. Another explanation for the low sperm counts in the late mating season is lower spermiation. Spermiation may occur to a lesser extent during the late mating season compared to earlier in the mating season. This would increase the amount of sperm males have available for transfer when a large number of receptive females are available. Spermiation varies seasonally in other fishes (*e.g.*, Jackson and Sullivan, 1995; Fauvel *et al.*, 1999; Caputo *et al.*, 2001; Kara *et al.*, 2007) and has been found to synchronize to oocyte production in gobies (*Aphia minuta*, Caputo *et al.*, 2001).

In conclusion, we found that reproductive investment varied seasonally in both male and female *Poecilia latipinna* in a population that occupies a constant temperature spring habitat. Contrary to other studies of livebearing fish, male *P. latipinna* reduced sperm availability during the nonmating season. Reduction in spermatogenesis is likely correlated to seasonal influences as well as the availability of gravid females. Further research is necessary to explore peaks in reproduction as well as how sperm limitation in females may vary by season.

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